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The Status of
The Great White Heron
[*ARDEA OCCIDENTALIS AUDUBON*]

AND

Würdemann's Heron
[*ARDEA WÜRDEMANNII BAIRD*]

By ERNEST G. HOLT

The Crile Florida Expedition

1923-1924



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THE CLEVELAND MUSEUM OF NATURAL HISTORY
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CONTENTS

	Page
Introduction	3
Historical Résumé	4
Field Notes	9
Data from Specimens	13
Behavior Differences	20
Distribution	24
Discussion	25
Summary and Conclusions	31
Bibliography	32



This first scientific publication of The Cleveland Museum of Natural History won the Walker prize in Ornithology "for marked merit" which was offered by the Boston Society of Natural History in 1926. The prize committee consisted of Messrs. E. F. Batchelder, Outram Bangs, and James Lee Peters, Fellows of the American Ornithologists' Union.—Ed.



GREAT WHITE HERONS
The brood of Nest No. 15, Northeast Buchanan Key, Florida Bay, January 4, 1924.

The Status of the Great White Heron

〔*Ardea occidentalis* Audubon〕

and Würdemann's Heron

〔*Ardea würdemannii* Baird〕

INTRODUCTION

For many years the true status of *Ardea occidentalis*, *Ardea würdemannii*, and *Ardea wardi* has been a moot question among ornithologists. Yet, whether *occidentalis* is a distinct species or only a white phase of *wardi*; whether *würdemannii* is a colored phase of *occidentalis*, a light phase of *wardi*, or a hybrid between the two; and whether *wardi* must be retired to the synonymy of *occidentalis*, are problems for which satisfactory explanations have not been advanced.

In December, 1923, and January, 1924, while serving with the Crile Florida Expedition of The Cleveland Museum of Natural History, I found the white and blue birds on the Florida Keys interbreeding freely; and, stimulated by these observations, I have made subsequent studies that, it is hoped, may contribute something towards a solution of the tangle in which these forms have become involved. If, however, the birds' relations appeared complicated in the field, where it seemed it must indeed be a wise child that could know its own father, the problem became complexity itself when I essayed a study of the series of skins collected.

I have not hesitated, therefore, to ask aid of others, and to these it is my pleasure to acknowledge my indebtedness. Mr. Waldron DeWitt Miller, of the American Museum of Natural History, and Mr. James L. Peters, of the Museum of Comparative Zoology, have kindly supplied measurements of certain specimens in their institutions; Mr. Arthur H. Howell, of the United States Biological Survey, has rendered a like service, and has also furnished data on the distribution of *Ardea occidentalis*, as well as various references; Dr. Charles W. Richmond, of the United States National Museum, has courteously loaned specimens, including the type, of *Ardea würdemannii*; Dr. Alexander Wetmore and Mr. Arthur Cleveland Bent have answered sundry queries; Messrs. R. M. Barnes, J. P. Norris, Jr., and T. Van Hyning have supplied data from their

collections of eggs; Messrs. Herbert L. Stoddard and Oather C. Van Hyning have placed unpublished records at my disposal; Professor H. D. Fish and Mr. J. L. Cartledge, of the University of Pittsburgh, have given aid and advice; Dr. Francis B. Sumner, of the Scripps Institution for Biological Research, has criticized the manuscript from the genetic viewpoint; and, lastly, I am under especial obligations to Mr. Rudyerd Boulton, of the Carnegie Museum, for preparing the maps reproduced herein, and to Mr. W. E. Clyde Todd, of the same institution, not only for extending the facilities of his laboratories for my studies, but as well for his counsel and encouragement during their prosecution.

HISTORICAL RÉSUMÉ

A thorough understanding of the questions at issue can be gained only by a careful study of the literature. Therefore, it is deemed best to preface my own thesis with a résumé of the treatment that previous writers have accorded the birds under discussion.

Audubon (1835b)¹ described *Ardea occidentalis* from a fine male that he secured near Key West in the spring of 1832. While in that region he procured a score of specimens and observed several hundred others alive in their natural haunts, and it is at once evident from his writings that the white birds impressed him as being entirely distinct from the large blue herons which occurred abundantly in the same locality.

Twenty years later, Bonaparte (1855) erected the monotypic genus *Audubonia* for this new species. Baird (1858) accepted *Audubonia*, but with reluctance, remarking, "It is very questionable whether this bird can be considered as entitled to separate generic rank, the differences from *Ardea* consisting only in a less extent of the feathers of head and scapulars, as well as in the white color."

In the same work, Baird described *Ardea würdemannii* from a specimen taken in "South Florida" by Gustavus Würdemann, of the United States Coast Survey. Of this new form Baird writes, "It has much the same size and proportions with the *Ardea*

¹ Complete references for the citations throughout the paper will be found in the Bibliography, pages 32-35.

occidentalis, and, in some respects, might almost be considered a cross between this species and *herodias*."

March (1864), writing on the birds of Jamaica, says of *würdemannii*, "The fishermen and gunners on the coast say this is the male of the preceding species [*herodias*] in summer plumage, but, from two specimens I have collected, I think they are quite distinct." He states that the great white heron is rare on the island.

Coues (1872) in the first edition of his Key to North American Birds, accords both *würdemannii* and *occidentalis* specific standing under *Ardea*, but remarks of the former that it seems improbable that it is anything more than a "special state" of *herodias*.

Ridgway (1878), in monographing the American species of *Ardea*, relegated *Audubonia* to the synonymy of *Ardea*, and recognized as inhabitants of Florida *herodias* and *occidentalis*. *Ardea würdemannii* was treated as a colored phase of *occidentalis*. In support of this position, the cases of the reddish egret, screech owl, little blue heron, and others are cited at considerable length as analogous examples. Two years later (1880), the same author published a statement that Dr. J. W. Velie, of the Chicago Academy of Sciences, while collecting in Florida, had "in two instances, once in 1872, and again in 1875, . . . found about half-grown young, one each of *A. occidentalis* and *A. würdemanni*, in the same nest!" "This evidence," says Ridgway, "is all that was needed to settle the question of the identity of the two forms in question, and there cannot now be any doubt that they represent two phases of one species, bearing to one another exactly the same relation as that between *Ardea rufescens*, Bodd., and *A. pealei*, Bonap."

In a third paper, published in 1882, Ridgway again takes up the vexed question of the Florida herons, and separates the great blue heron of southwestern Florida as a distinct species which he calls *Ardea wardi* in honor of Charles W. Ward, who collected the type at "Oyster Bay."² He summarizes the status of the species thus:

"There are hence several hypotheses which might be plausibly

² The name of the type locality is actually Estero Bay (cf. Holt, The Auk, XLII, 1925, p. 266).

argued upon theoretical grounds, and which may be stated as follows: (1) That *A. occidentalis*, *A. würdemanni*, *A. wardi*, and *A. herodias* all belong to a single species, which reaches its extremes of variation in the first- and last-named; (2) That these names include three distinct races or species: *A. herodias*, which is never white; *A. occidentalis*, which is dichromatic (having separate white and colored phases), and *A. wardi*, also dichromatic, its white phase indistinguishable from that of *A. occidentalis*, and its colored phase distinguishable from that of the same species (*A. würdemanni*) by the different pattern and color of the head and neck alone; and (3) that there are two species, *A. occidentalis* and *A. herodias*, which in Florida hybridize on an extensive scale, producing the intermediate specimens which have been distinguished as *A. würdemanni* and *A. wardi*.

"Of these hypotheses I have, after careful consideration of them all, concluded to adopt the second as being most consistent with known facts."

The collector of the type of *Ardea wardi*, however, did not agree with Ridgway's assumption that the species is dichromatic, for in 1884 Ward wrote, "It would appear from all the evidence at my command that *A. wardi* has no white phase. The only evidence tending to substantiate the theory of dichromatism is the finding of a white and gray bird in the same nest at Estero Bay in 1881, and the bird procured last March, on Kissimme Lake, with the white occipital plume. This would seem to be insufficient."

The same year, 1884, marked the appearance of Baird, Brewer, and Ridgway's Water Birds of North America. In it *occidentalis*, *wardi*, and *herodias* are each accorded specific rank and *würdemannii* is considered the colored phase of the first. It is stated, "The identity of *Ardea Würdemanni*, Baird, with *A. occidentalis*, Audubon, although not proven, is inferred from a number of circumstances and coincidences in the history of each, which, together with their entire similarity of size and form, render it extremely probable that the case of *Ardea rufa*, Boddaert, and *A. 'Pealei'*, Bonaparte, is repeated in the present instance; these two supposed species in all probability being, as has been incontestably proven with *rufa* and '*Pealei*', 'dichromatic' phases of the same species." However, it is said further, "Mr. N. B. Moore deems it

highly probable that the birds now standing as *A. Würdemanni* may prove to be only a rare and elegant variety of *herodias*." Ridgway's opinion of 1882, that *wardi* also is dichromatic, is here retained.

Ridgway (1887a) reported on eight specimens of *würdemannii* taken by R. C. Stuart in December, 1886, on the keys near Cape Sable. After describing the specimens, one of which was said to be "clearly intermediate between *A. wuerdemanni* and *A. wardi* and may possibly be a hybrid between the two," the author remarked: "What relationship *Ardea wuerdemanni* bears to *A. occidentalis* and *A. wardi* the material examined does little toward elucidating. It would seem to be a permanent form, however, and, if not a color-phase of *A. occidentalis*, is probably a distinct species." In fact, the same author, in his Manual of North American Birds, published that same year, accorded full specific rank each to *occidentalis*, *würdemannii*, *wardi*, and *herodias*.

Scott (1889), who has written much on the birds of Florida, also considered *occidentalis*, *würdemannii*, and *wardi* as distinct species. He, too, secured a specimen which he believed to be a hybrid between the last two.

Coues (1894), in the fourth edition of his Key to North American Birds, states that *occidentalis* is similar to *herodias*, but larger and dichromatic; and describes first the colored phase under the parenthetical name of *würdemanni* Baird. In this, he follows Baird, Brewer, and Ridgway (1884), but *wardi* is relegated to a note stating that it is indistinguishable in its white phase from *occidentalis* and is exactly like *occidentalis* in its colored phase except that the head is colored as in *herodias*.

Maynard (1896) assigned specific rank each to *würdemannii* and *occidentalis* in the revised edition of his Birds of Eastern North America, but omitted any reference to *wardi*. This comes about very probably because the first edition of that work was published before *wardi* was described, and the subsequent revision was imperfect. There is no doubt, however, that Maynard considered the great white herons and the great blue herons of Florida as essentially different birds.

Ridgway, who had given more thought to Würdemann's heron than any other author, well reflected the quandary in which he

found himself in 1896 by again shifting his ground. This statement appears in the second edition of his Manual of North American Birds: "*A. wuerdemanni* is probably merely an intermediate plumage connecting *A. occidentalis* with *A. wardi*, the three forms doubtless merely color-phases of one species, for which *A. occidentalis* is the older name."

In 1901, Chapman described a new race of the great blue heron and, upon the basis of material brought together incident to that study, relegated *wardi* to a subspecific position under *Ardea herodias*.

However, the fifth edition of Coues' Key to North American Birds (1903), rates *wardi* as a full species alongside *herodias*, *würdemannii*, and *occidentalis*, though it is stated of *wardi* that it "may be a local race of *herodias*, or the result of interbreeding between *herodias* and *occidentalis*." Further, "A slight strain of *occidentalis* running in *herodias* might produce *wardi*; and subsequent admixture of *wardi* with *occidentalis* might result in *wuerdemanni*. But doubtless this form should stand as *A. h. wardi*." The status of *würdemannii* is considered questionable and it is said that it might be the colored phase of *occidentalis*, "or a possible hybrid between *occidentalis* and *herodias*."

Bent, writing in 1904, has given interesting accounts of *A. occidentalis* and *A. herodias wardi* in the Cape Sable region and plainly considers the two forms quite distinct. *A. würdemannii* is not mentioned.

In the revised edition of Chapman's Handbook of Birds of Eastern North America (1912), *occidentalis* is accorded full specific rank and to the account of the species is appended this paragraph:

"*Ardea wuerdemanni* Baird has been considered to be a color phase of this species, but its true standing is unknown. It may be described as a Ward's Heron with a whitish head and neck, and is thus intermediate between *occidentalis* and *wardi*. On March 27, 1908, on Clive Key, southeast of Cape Sable, I found two young Ward's Herons and one pure white bird in the same nest. One of the parents was *Ardea occidentalis*, the identity of the other was not ascertained."

Oberholser (1912) regards "*Ardea herodias* as specifically dis-

tinct from *Ardea occidentalis*; *Ardea wardi* the Florida subspecies of *Ardea herodias*; *Ardea occidentalis* a distinct species; and *Ardea würdemannii* a hybrid between *Ardea herodias wardi* and *Ardea occidentalis*."

Bangs (1915), however, reasoning from the supposed analogies furnished by the reddish egret, reef heron, and little blue heron, very positively takes the opposite stand and proposes that *Ardea herodias wardi* and *A. würdemannii* be retired to the synonymy of *Ardea herodias occidentalis* Audubon.

To Bangs' dictum Bartsch (1917) takes exception and says that no one who knows the great white heron and the great blue heron in the field would believe that they were the same.

Howell, who has had extended field experience in Florida, supports the last view; and in a recent paper (1921) lists *occidentalis* as a separate species.

Barbour (1923), in his Birds of Cuba, follows Bangs by treating the great white heron of the island as a phase of *Ardea herodias repens*.

Bailey (1925) writes: "I have occasionally seen in their rookeries, a large blue heron as a mate to a great white, and have also seen both white and blue phase young in the same nest. I attribute this, not to two forms pairing, but believe that there is a blue phase in the 'Great-whites', just as there is a white phase of the Little-blue-Heron and Reddish Egrets. The more I see of color 'phases' in the Little-blue and Great-white, the more I'm inclined to think that they do not reach the natural color with age, as many suppose; and that many 'Little blue' retain the white plumage for all time. And *vice versa*."

And, finally, Bent (1926) expresses the conviction that *Ardea occidentalis* is a perfectly distinct species, and that *Ardea würdemannii* is a hybrid between it and *Ardea herodias wardi*.

FIELD NOTES

Unfortunately, this chaotic condition of affairs was not realized until my return from the field; and, consequently, believing that I was witnessing a simple case of hybridization, I failed to make the most of the opportunity for an intensive study of differential

behavior. The observations that were made, however, are not without some importance.

In every phase of my field work, from spying upon the private affairs of herons to skinning specimens, I received the whole-hearted support and assistance of the entire Crile party. In my experience it has been a rare thing indeed to find anyone with the enthusiasm to endure day after day the discomforts of mud flats and mosquito-infested blinds for the doubtful satisfaction of knowing whether a blue bird had a white father. It requires, too, sportsmanship of a high order to smile cheerfully when one's house-boat becomes completely saturated with such odors as only half-cured heron skins can produce. Therefore it gives me peculiar pleasure to express here my sincere admiration and esteem for Dr. and Mrs. George W. Crile, their sons, George Harris and Robert, and their nephew, Henry Sherman; and my grateful appreciation of the help and kindness that they tendered me at every turn. I am indebted to Dr. Crile, too, for the generosity that made it possible for me to take part in his expedition, and that now permits the publication of this paper.

In the late afternoon of December 23, our cruising house-boat put out for Miami, and turned southward among the quiet channels between the mainland and the Florida Keys. Next day we anchored off Angelfish Key, and there saw five Ward's herons. The first great white heron was seen on Christmas on a mud bank on the seaward side of the same island; on the same day three Ward's herons were recorded. The next record is of a great white heron seen at "Ferguson's Rookery", opposite Long Island, on December 27. It is thus apparent that the white birds were anything but common on the upper keys.

On December 28 we visited the Buchanan Keys in Florida Bay; and here, to my astonishment, young herons were found almost ready to leave the nest. In fact, young birds of such size were so unexpected that I actually shot three standing upon their nest before realizing that they were not adults perched upon the dense foliage. The eggs from which these birds came must certainly have been laid not later than October.

The Buchanan Keys comprise three small islands, elevated but little above mean high tide (see Plate II). The two larger are



FIG. 1. WESTERN SHORE OF NORTHEAST BUCHANAN KEY
The black mangroves at the left furnished nest sites for both great white and Ward's herons.



FIG. 2. SHORE LINE OF SOUTHWEST BUCHANAN KEY
These dense marginal tangles of mangroves were inhabited by cormorants and pelicans as well as herons.



FIG. 1. A MIXED BROOD

The single blue and two white young of Nest No. 2, Middle Buchanan Key, December 28, 1923.



FIG. 2. GREAT WHITE HERON BROOD OF NEST No. 4

One bird has met a tragic death by falling and entangling a foot among the branches. Middle Buchanan Key, December 28, 1923.

comparatively dry in the center, and somewhat open there; but one landing upon such a key must struggle through a dense fringe of red mangroves and then through an inner belt of black mangroves before reaching the comparatively open center. Everywhere underfoot there was a thick mat of saltwort (*Batis maritima*). The black mangroves (*Avicennia nitida*) were unquestionably the favorite nesting sites of the herons.

A careful search of Middle Buchanan Key on December 28 revealed six nests of young herons. Three of these nests (one shown in Plate IV, fig. 1) each contained three young great white herons. Nest No. 4 (Plate III, fig. 2) harbored four young great white herons (though one had tripped and was hanging head-downwards, dead) which were visited on three different evenings by a single white parent. In another nest were two blue young and to this nest there came one evening a great white heron, but did not feed the young. The most interesting of this group, however, was Nest No. 2 (Plate III, fig. 1). It held one blue and two white nestlings. Contour-feathers were well developed and the birds were able to stand, though the white birds were larger than the blue one and their plumage farther advanced. On December 30 a blind was constructed near this nest, and from it a blue female (C.M.N.H. No. 1765) was shot when she came home at evening. Next day the nest was watched from 5:15 to 6:45 p. m., but the other parent never appeared, and the young were collected for a group.

Southwest Buchanan Key, only a tiny islet, yielded four nests. The first contained two white and two blue young, and to it came a single great white heron parent, but no specimens were taken. In the next nest were three white young, and on the ground beneath another lay dead. The third nest held three blue young, visited by a blue adult; while the last nest contained two white young.

On Northeast Buchanan Key, January 4, 1924, we found nine nests which contained, respectively: 1 blue nestling; 2 blue nestlings; 2 white nestlings; 4 eggs; 3 white nestlings (Frontispiece), from which one white parent was flushed; 1 blue nestling almost grown and 1 fresh egg; 2 white nestlings; 1 white nestling (Plate IV, fig. 2); and 3 white nestlings. When the island was visited the next afternoon only the nest of eggs and the brood of two blue

nestlings remained. The fresh mark of a prow on the muddy shore, a trail through the saltwort, some empty cartridges, and clots of blood beneath the nests told the story. Evidently the "conchs" had wearied of a diet of fish.

Barnes Key—essentially like those preceding, only larger, and but a mile or two distant—was explored on December 31; and on it were found three heron nests. The first contained 3 blue young nearly grown; the second, 2 blue young; and the third, 2 downy white young, 1 downy blue young, and a pipped egg.

The small southeast island of Bowlegs Keys on January 1, 1924, harbored eight nests containing, respectively: 4 white young; 3 white young; 2 white young; 2 downy white young (collected with the white mother, C.M.N.H. No. 1397, for a group); 4 great white heron eggs; 4 great white heron eggs (white parent flushed); 4 Würdemann's heron eggs (Nest No. 23, collected with adult male, C.M.N.H. No. 1767, which was flushed from the nest); and 4 unidentified eggs.

Our last visit to these lower keys was on January 5. January 9 found me back in Miami preparing to go into the Everglades. Between January 12 and 30, Ward's herons were often seen in the lower Everglades and the coastal swamps, frequenting drainage canals and small lakes. Great white herons, however, were conspicuously absent from this region, and were seen on the mainland only along the canal near Ingraham and Gator Lakes, and on Gator Lake. Only four individuals all told were recorded here.

But the keys just off Cape Sable presented a very different picture. About them, on the extensive mud banks bared at low tide, great white herons stood like statues of purest alabaster, clean-cut, and visible for remarkable distances. During periods of high tide they resorted to the trees on the islands. Large blue herons were common here, too; and, in fact, outnumbered the great white herons—which was not the case on the keys farther south. And, unlike the condition on the lower keys, the great white herons here seemed to have finished breeding. On East Oyster Key, January 20, a single fledgling was found, out of the nest but still unable to fly; and on the same day on West Oyster Key a flying immature bird was mistaken for an adult, and collected.

On the other hand, the big blue herons were still nesting. An



FIG. 1. GREAT WHITE HERON BROOD
Nest No. 5, Middle Buchanan Key, December 28, 1923.



FIG. 2. YOUNG GREAT WHITE HERON
Nest No. 18, Northeast Buchanan Key, January 4, 1924. This bird illustrates very well the immaculateness of the white young.

unnamed key off Cape Sable on January 18 sheltered four nests which contained: 3 downy young; 2 recently hatched young and 1 pipped egg; 2 young almost ready to fly (visited by a blue parent); and 2 downy young and 2 eggs (1 pipped). Clive Key was found on January 20 to hold four nests containing: 2 downy young and 2 eggs (1 pipped); 3 small nestlings; 3 small nestlings; 2 young just hatched and 2 eggs (1 pipped). On the same key was taken the palest blue heron (C.M.N.H. No. 1407) secured on the entire trip. Its head is white, and the entire bird is lighter than the type of *Ardea würdemanni*.

A single big blue heron's nest on East Oyster Key, containing 2 eggs and 1 young just hatched, and from which a blue parent was flushed, completes the list of nests examined on the keys.

To summarize: A total of 40 nests were examined on Buchanan, Barnes, Bowlegs, Clive, and Oyster Keys, and an unnamed key near the last; and found to contain 48 young white herons, 38 young blue herons, and 31 eggs. Forty-seven of the white nestlings were found on Buchanan, Barnes, and Bowlegs Keys; one on East Oyster Key. Eighteen blue nestlings lived on Buchanan and Barnes Keys; 20 on the Cape Sable group. Among the adults was shown the same tendency of the white birds to predominate on the lower keys, and of the blue birds to be more numerous on the upper keys. Of the 40 nests examined, 3 held mixed broods of white and blue nestlings in the ratio of 2:1, 2:2, and 2:1. The first had a blue parent, the second a white parent; the parent of the last was not seen. The mixed broods were found on Buchanan and Barnes Keys, but all the adult blue herons collected on any of the keys showed admixture of white blood.

My next field of action was the Kissimmee Prairie, near Bas-senger. Here Ward's herons were very numerous; but great white herons were, of course, entirely absent. Moreover, no Ward's herons seen showed any departure from the limits of variation to be expected in *Ardea herodias wardi*.

DATA FROM SPECIMENS

We come now to a consideration of the specimens in hand. My own Florida collections number 11 white and 14 blue herons. Beside these I have personally examined the specimens in the

Carnegie Museum, and the type and 2 topotypes of *Ardea würdemannii* from the United States National Museum. In addition, specimens, in the Museum of Comparative Zoology, the American Museum of Natural History, and the United States National Museum, have been examined for me by the gentlemen already mentioned. Rigidly excluding all birds not fully adult, there remain for critical comparison 24 great white herons, 24 Ward's herons, and 10 specimens which may for convenience be termed *würdemannii*. I have also carefully examined in the laboratory 6 juvenal great white herons and 6 juvenal and immature blue herons, though their measurements are not used in comparison. Several dozen nestlings of each species were seen in the field.

At the very outset I was struck by the immaculateness of the great white herons. Only two of my own birds show the slightest trace of color, and that is limited to a few scattered feathers (the longest only 21 mm. in length) of dusty brown on the forehead of C.M.N.H. No. 1397, an adult female from Bowlegs Keys; and to a single feather with brownish base on the forehead of C.M.N.H. No. 1393, an adult female from Clive Key. The former was the mother of two nestlings, neither of which shows any color whatever. Nor do any of four other juvenals at my disposal, including one from the Isle of Pines, show any color. In the field, moreover, it was noticed that white nestlings were always devoid of any colored feathers. This is very well shown by the photographs which are here reproduced. Of the specimens examined for me by others, only one is reported to show color—U.S.N.M. No. 110675, an adult male from Cape Sable, which has the tips of some of the secondaries washed with pallid neutral gray for about three-quarters of an inch. Scott (1889) mentions two Würdemann's herons "in the white phase" which were "pure white everywhere except on the last two or three inches of their outer primaries, which were in color blue and marked much like the primary quills of *Ardea cærulea* in its white phase of plumage."

Another noticeable feature of the white birds is the reduction, often total absence, of the occipital plumes. Only 9 of the 24 birds listed in Table I have plumes over 100 millimeters in length, whereas more than half possess no plumes at all. These plumes, when present, are wide at the base and taper to a fine point—a

form perhaps best described as long acuminate-lanceolate—and are quite different from the two long, ligulate occipital plumes of *Ardea herodias wardi*. The length of the longest occipital feather of 24 Ward's herons is shown in Table II. From Table III, where the averages of Tables I and II are compared, it will be noted that there is an average difference between the two species of 80.5 mm., or more than 3 inches. The opposing series of specimens are wholly comparable, as all are from Florida, all are fully mature, and all were taken during the breeding season (as shown by the dates in the tables).

The scapular and jugular plumes of the great white heron also show a tendency to reduction when compared with similar structures of Ward's heron. However, these plumes, unlike the occipital plumes, present no great differences in form between the two birds. Audubon's Plate No. 281 (Birds of America, 1835) depicts "a remarkably large" adult male, but without scapular plumes, with no strap plumes from the occiput, and with jugular plumes widened and flattened—not rod-like as in *wardi*. Young birds taken to Charleston by Audubon (Ornithological Biography, 1835, p. 547) and kept for more than a year did not develop occipital plumes. Baird (1858) and Coues (1872) both remark that there are no greatly elongated occipital feathers or lengthened scapulars.

A small but distinct difference between *occidentalis* and *wardi* in absolute and proportionate size of bill is indicated by the measurements of the six fully adult *occidentalis* in hand when compared with similar measurements tabulated by Oberholser (1912) for six entirely comparable Florida specimens of *wardi*. The average lengths of wing, tail and tarsus in this series are greater for *wardi* than for *occidentalis*, whereas the bill averages longer and thicker in *occidentalis*. Of course, in such an insignificant series, averages can not be more than suggestive; but it is noteworthy that the suggestion of proportionately longer and heavier bill in *occidentalis* is materially strengthened by closer analysis of the figures. When the length of culmen is divided by the length of tarsus the quotient gives an index of proportion that is very constant and which quite sharply separates the two species, the index for *wardi* falling always definitely below that of *occidentalis*. This suggests that an ade-

quate series of measurements (unfortunately not at my command) would establish proportionate size of bill as a diagnostic character upon which alone these two species could be separated.

Of the 14 blue birds that I collected, 7 are juvenal or immature, but the remaining 7 are fully grown and worthy of detailed consideration. These are listed in Table IV, where also will be found listed the 3 specimens of *würdemanni* (including the type) borrowed from the United States National Museum. The latter have been so well described by Ridgway (1878 and 1887) that further notice here is unnecessary.

TABLE I
Ardea occidentalis
(Adults only)

Number	Locality	Date	Sex	Longest occipital feather mm
M.C.Z. 219809	Cape Sable, Florida.....	Dec. —	♂	169
M.C.Z. 246697	Key West, Florida.....	Dec. 4	♂	104
M.C.Z. 246698	Key West, Florida.....	Dec. 17	♂	169
M.C.Z. 246699	Key West, Florida.....	Dec. 19	♂	66
M.C.Z. 207887	Cedar Keys, Florida.....	Jan. 1	♂	158
M.C.Z. 229215	Key West, Florida.....	Mar. 9	♂	79
M.C.Z. 246715	Key West, Florida.....	May 25	♂	192
U.S.N.M. 110675	Cape Sable, Florida.....	Dec. 27	♂	71
U.S.N.M. 6540	Indian Key, Florida.....	Mar. 18	♂	53
U.S.N.M. 110695	Nameless key off Cape Sable.....	May —	♂	75
C.M.N.H. 1395	West Oyster Key, Florida.....	Jan. 18	♂	65
Average of 11 males.....				109.2
M.C.Z. 246700	Key West, Florida.....	Dec. 17	♀	140
M.C.Z. 219810	Cape Sable, Florida.....	Dec. —	♀	126
M.C.Z. 42534	Sand Key, Florida.....	Apr. 16	♀	66
Sanford Coll.	Florida.....		♀	95
U.S.N.M. 269254	Naples, Florida.....	Apr. 1	♀	54
U.S.N.M. 110696	Nameless key off Cape Sable	May —	♀	67
Car.Mus. 94832	Cape Sable, Florida.....	Mar. 13	♀	59
Car.Mus. 94889	Bear Lake, Florida.....	Mar. 27	♀	65
C.M.N.H. 1397	Bowlegs Keys, Florida.....	Jan. 5	♀	76
C.M.N.H. 1393	Clive Key, Florida.....	Jan. 18	♀	113
C.M.N.H. 1394	West Oyster Key, Florida.....	Jan. 18	♀	104
Average of 11 females.....				87.7
M.C.Z. 46874	Florida.....		?	76
Sanford 6413	Florida.....		?	94
Average of 2 of unknown sex.....				85.0
Average of all specimens.....				97.3

TABLE II
Ardea herodias wardi
(Adults only)

Number	Locality	Date	Sex	Longest occipital feather mm
Car.Mus. 27428	Polk Co., Florida.....	Feb. 18	♂	195
M.C.Z. 229216	Tarpon Springs, Florida.....	Jan. 15	♂	192
M.C.Z. 72855	Kissimmee River, Florida.....	Jan. 18	♂	118
M.C.Z. 229217	Tarpon Springs, Florida.....	Feb. 15	♂	201
M.C.Z. 110596	Seven Oaks, Florida.....	Mar. 1	♂	182
M.C.Z. 229220	Tarpon Springs, Florida.....	Mar. 2	♂	190
M.C.Z. 229221	Tarpon Springs, Florida.....	Mar. 2	♂	200
M.C.Z. 230502	Banana Creek, Florida.....	Mar. 11	♂	229
M.C.Z. 42537	Smyrna, Florida.....	Mar. 22	♂	227
M.C.Z. 42538	Smyrna, Florida.....	Mar. 24	♂	230
A.M.N.H. 3553	Tarpon Springs, Florida.....	Mar. 2	♂	197
A.M.N.H. 49599	Suwannee River, Florida.....	Mar. 21	♂	159
A.M.N.H. 99101	Micco, Florida.....	Apr. 8	♂	92
U.S.N.M. 152879	Lake Harney, Florida.....	Dec. 28	♂	155
U.S.N.M. 162577	Palatka, Florida.....	Jan. 27	♂	115
U.S.N.M. 175423	Lake Hatch-me-haw, Florida.....	Feb. 14	♂	190
U.S.N.M. 175531	Kissimmee River, Florida.....	Mar. 9	♂	203
U.S.N.M. 77946	Hernando County, Florida.....	Mar. 30	♂	183
Average of 18 males.....				181
M.C.Z. 38916	Punta Rassa, Florida.....	Mar. —	♀	208
A.M.N.H. 36981	Rutland, Florida.....	Jan. 15	♀	90
A.M.N.H. 99102	Micco, Florida.....	Apr. —	♀	148
U.S.N.M. 152148	Ft. Bassenger, Florida.....	Feb. 18	♀	170
Average of 4 females.....				154
U.S.N.M. 126114	San Mateo, Florida.....	Mar. 29	?	183
U.S.N.M. 90021	Gainesville, Florida.....		?	210
Average of 2 of unknown sex.....				196.5
Average of all specimens.....				177.8

TABLE III
Comparative Averages
Length of Longest Occipital Feather In Millimeters

	Adult Males Specimens	Average	Adult Females Specimens	Average	Adults of ? sex Specimens	Average	All Specimens Number	Average
<i>Ardea occidentalis</i> .	11	109.2	11	87.7	2	85	24	97.3
<i>Ardea herodias wardi</i> .	18	181	4	154	2	196.5	24	177.8
Difference.	..	71.8	..	66.3	..	111.5	..	80.5

TABLE IV
“*Ardea würdemanni*”
(Adults only)

Number	Locality	Date	Sex	W. mm	T. mm	Cul. mm	Bill mm	Tar. mm	Longest Color of bill occip. feather plumes
U.S.N.M. 8690 (Type)	South Florida.....	♂	51.5	182	164	32	204	95 White
U.S.N.M. 10210	Cape Sable, Florida.....	♂	472	172	153	33	190	126 White
C.M.N.H. 1767	Bowles Keys, Florida.....	Dec. 1	♂	515	186	159	31	210	92 White
C.M.N.H. 1405	Man-O'-War Key, Florida.....	Jan. 2	♂	471	175	156	31	200	65 Black
*C.M.N.H. 1408	East Oyster Key, Florida.....	Jan. 18	♂	485	180	151	33	197	168 Black
Average.....	492	179	157	32	200	109
U.S.N.M. 110211	Cape Sable, Florida.....	Dec. 1	♀	480	174	162	35	196	166 White
C.M.N.H. 1765	Buchanan Keys, Florida.....	Dec. 30	♀	465	167	149	29	180	136 Mixed
C.M.N.H. 1409	Unnamed key off Cape Sable, Florida.....	Jan. 18	♀	440	165	144	30	180	125 Mixed
C.M.N.H. 1410	Unnamed key off Cape Sable, Florida.....	Jan. 18	♀	462	174	142	31	187	110 Mixed
*C.M.N.H. 1407	Clive Key, Florida.....	Jan. 20	♀	463	168	148	30	190	148 White
Average.....	462	170	149	31	187	137

*Almost typical *wardi*.

†Oldest specimen of the collection.

NOTE: Measurements were taken according to the methods used by Oberholser (1912).

In the order named, C.M.N.H. Nos. 1408, 1405, 1409, 1765, 1767, 1410, and 1407 indicate progressive admixtures of white blood, from the first, which is almost normal (third outer primaries tipped with paler), to the last, which is paler even than the type of *würdemannii*. All, except Nos. 1405 and 1767, have some pale-tipped primaries—the two palest birds having the most extensive pale areas on these remiges. The longer jugular plumes of the hybrids tend to lose the vinaceous wash of the pure-blooded blues, and become white. No. 1408, which seems to have the least white blood, has the black ligulate occipital plumes typical of pure *wardi*, except that they are shortened, and widened at the base. In the other six hybrids these plumes are even more reduced, and are paled, becoming pure white with a bit of black at the tip in No. 1407. The occipital plumes of U.S.N.M. Nos. 8690 (type), 110210, and 110211 are pure white, although those of the last are washed at the base with pale vinaceous gray. It is noteworthy that the occipital plumes of the birds of mixed blood are sometimes acuminate-lanceolate and sometimes ligulate in form, as the wearer evidences more or less admixture of white blood. This change of form is directly correlated with the change of color of the plume; that is, the whiter the plume the more lanceolate, and vice versa.

An adult female, C.M.N.H. No. 1765, taken with its brood of three nestlings on Buchanan Keys, presents evidence of mixed blood in the paling of greater coverts, tibiæ, and tips of some primaries, in a gray feather among the occipital plumes, and in the shortening of these plumes. One of its nestlings (C.M.N.H. No. 1402) is a blue bird too young for anything to be determined from a study of its plumage; the other two (C.M.N.H. Nos. 1400-1401) are pure white without a trace of color!

The palest bird examined, C.M.N.H. No. 1407, from Clive Key, is paler in every respect, except the neck, than a pure specimen of *wardi* (Car. Mus. No. 27428) from Polk County. The back is not only paler, but has a distinct vinaceous wash. Because of the old, stained condition of the type of *würdemannii*, it is difficult to determine whether it also once possessed such a cast. The present bird compares with the type in the small amount of black on the sides and its almost total absence from the belly, but the

tibiae are even paler than in the type, being hardly darker than rufous buff. The first five outer primaries are pale at the tips—not so in the type. The head is whiter than the type, and there is less brown streaking on the forehead. The occipital plumes are longer; one is dusky, the other white with black shaft-streak at tip. The tarsi are reddish rather than blackish as in unmixed birds.

Yet even this very pale specimen is distinctly a blue bird, and between it and the white birds there is an enormous gap that does not begin to be bridged by the few dusky feathers found on the white birds mentioned. Neither is there any evidence of spotting.

In this study, skins of both *Ardea herodias herodias* and *Ardea herodias wardi*, from points removed from the Florida Keys, were examined; but these forms have been so thoroughly considered by Oberholser (1912) that it is only necessary to note here the fact that in no specimen of either has there been seen any paling of colors or shortening of occipital plumes such as is observed in the 10 specimens of *würdemannii* just discussed. Conversely, every blue bird I took on the Florida Keys exhibited these modifications. This indicated that such phenomena occur only where the range of *wardi* overlaps that of *occidentalis*. Moreover, in that area, modification of the blue form seems to be the rule, for in a series of 19 birds in "very fine, unworn, adult plumage" Scott (1889) found that a very considerable percentage had "some of the long occipital plumes not wholly black, but blue or whitish."

The eggs of *occidentalis* and *wardi*, examined in series, are said to be indistinguishable. However, those of *occidentalis* that I collected are larger than the eggs I took of the big blue heron in the same region, and those of one set of the former are larger than any of *wardi* that I have seen. My *wardi* (or *würdemannii*) eggs from the Florida Keys show the same rounded elliptic form as the eggs of *occidentalis*; but *wardi* eggs I took at Bassenger are all more pointed, usually at both ends. Nevertheless, I would not be understood as placing more than suggestive value upon these slight differences in eggs.

BEHAVIOR DIFFERENCES

It seems to be very generally declared by those who have had

most experience with the great white heron in the field that in life it is a very different bird from its big blue associate.

The earliest account we have of the bird, of course, is that of its discoverer, Audubon (1835b). On April 25, 1832, Mr. Egan brought to Audubon at Indian Key two young great white herons about three weeks old—the first that he had ever seen of the species. On the 26th another live bird, out of the nest but unable to fly, was secured and liberated in the yard with the first two. "On seeing it," Audubon tells us, "the latter immediately ran towards it with open bills, and greeted it with a most friendly welcome, passing their heads over and under its own in the most curious and indeed ludicrous manner." These birds "thrived well, and never manifested the least animosity towards each other."

Evidently this fraternal spirit did not extend to herons not of their own blood, for "one of them which accidentally walked before the coop in which the Blue Herons were, thrust its bill between the bars, and transfixes the head of one of these birds, so that it was instantaneously killed." When leaving Key West, Audubon had two other young great white herons and also two young *Ardea herodias* alive. "After bringing them on board," he writes, "I placed them all together in a very large coop; but was soon obliged to separate the two species, for the white birds would not be reconciled to the blue, which they would have killed. While the former had the privilege of the deck for a few minutes, they struck at the smaller species, such as the young of *Ardea rufescens* and *A. Ludoviciana*, some of which they instantly killed and swallowed entire, although they were abundantly fed on the flesh of green Turtles."

Four of the young great white herons arrived in Charleston alive, but their fierce disposition wrought their undoing. They "struck at chickens, grown fowls and ducks, which they would tear up and devour. Once a cat which was asleep in the sunshine, on the wooden steps of the veranda, was pinned through the body to the boards, and killed by one of them. At last they began to pursue the younger children of my worthy friend [John Bachman], who therefore ordered them to be killed." Maynard (1896) also remarks upon the fierceness of the great white heron, saying, "The young bird which I captured, proved so untamable and

savage, striking at everything that came near, that I soon gave it its liberty." Similar complaints have not been lodged against the Ward's heron.

Truculent as the great white heron may be in captivity, in its natural environment it has been found very wary. Audubon (1835b) writes: "This species is extremely shy. Sometimes they would rise when at the distance of half a mile from us, and fly quite out of sight. . . . Indeed, I have no doubt that half a dozen specimens of *Ardea Herodias* could be procured for one of the present, in the same time and under similar circumstances." Seemingly all other observers are in agreement with Audubon on this phase of the character of the great white heron. Bryant (1859) says, "They are by far the wildest birds of the genus that I am acquainted with." Scott (1890) found them "so wary as to be almost impossible to approach, even when nesting." According to Maynard (1896), "... the Great Whites are, beyond all doubt, the shyest of the Herons," and he found it "often quite impossible to go within half a mile of them." Bent (1904) speaks of the species as "the grandest, the handsomest, and the shyest of its tribe." He says the birds "will fly at the sight of an approaching boat half a mile away. It is almost as difficult to approach them on land, even under the cover of the mangroves, where the slightest noise will send them flying away croaking hoarsely." Of the Ward's heron, he says, "In general habits it closely resembles its northern relative, but it is not so shy as the Great Blue and not nearly as difficult to stalk as the Great White Heron."

Writers are in accord, too, on the bearing of the great white heron. Audubon (1835b) says, "These Herons are sedate, quiet and perhaps even less animated than the *A. Herodias*. They walk majestically, with firmness and great elegance." Bent (1904) writes, "In all their movements they are deliberate and dignified; in flight they are slow, direct and powerful."

However, Audubon's statement (1835b) that "they flock at their feeding grounds, sometimes a hundred or more being seen together," is not corroborated by later writers. Bryant (1859) "never saw more than five or six individuals feeding near each other," and thought the great white heron "as much more solitary in its habits than the Great Blue Heron as the latter is than the

majority of other species." Scott (1890) says the great white heron seemed "to be of a solitary disposition, in no way resembling its allies, all of which seem more or less gregarious, especially in the breeding season. An examination of the keys rarely showed the existence of more than two nests on an island." Bent (1904) remarks that "it is no uncommon sight to see ten or twelve of these great birds standing in the shallow water around the shores of some small estuary," and describes a breeding colony which contained four nests. But no one since the days of Audubon seems to have seen flocks that would number a hundred birds.

Audubon (1835b) found another and, if true, important difference in the habits of the great white heron and the Ward's heron, that is, the time of feeding. Of the former he writes, "They seem, in so far as I could judge, to be diurnal, an opinion corroborated by the testimony of Mr. Egan, a person of great judgment, sagacity and integrity." On the other hand "the Blue Heron feeds at all hours of the day, as well as in the dark and dawn, and even under night." Baird, Brewer, and Ridgway (1884) repeat Audubon's statement regarding the great white heron, and say that the great blue heron is "diurnal as well as nocturnal," and "will venture even more fearlessly forth at night in quest of food."

Bartsch (1917), while not entering into particulars, states emphatically, "The Great White Heron of the Keys is so entirely different in its habits and psychological manifestations from the Great Blue Heron which occupies the same region that no one who knows the two birds in the field would believe that they were the same."

I myself made no notes of differential traits, for, as already intimated, the birds seemed to me to be too distinct to require such a study. In default of such notes this section is closed with quotations from a letter from Mr. A. C. Bent, who for years has been a close student of Florida bird-life.

"The living birds are quite unlike, and I do not see how anyone who is familiar with the two in life can fail to recognize them as distinct species. Although their ranges overlap, they are not coincident. *A. herodias* (and even *A. herodias wardi*) has a wide range, in most of which *occidentalis* is not found. *A. occidentalis* occupies a strictly maritime habitat, seldom wandering inland

from the seacoast. It lives, feeds, and breeds on, in or near salt water. *A. herodias* is common inland. I have never seen *occidentalis* in fresh water lakes, and have never known it to nest on the mainland.

"*A. herodias* in southern Florida is very tame, almost absurdly so, whereas in the same region *A. occidentalis* is one of the shyest and wariest birds I have ever seen. Its behavior is quite different. I think the two species are closely enough related to interbreed, with fertile offspring (as is the case with the black duck and the mallard), and thus produce the hybrids known as *A. wuerde-manni*."³

DISTRIBUTION

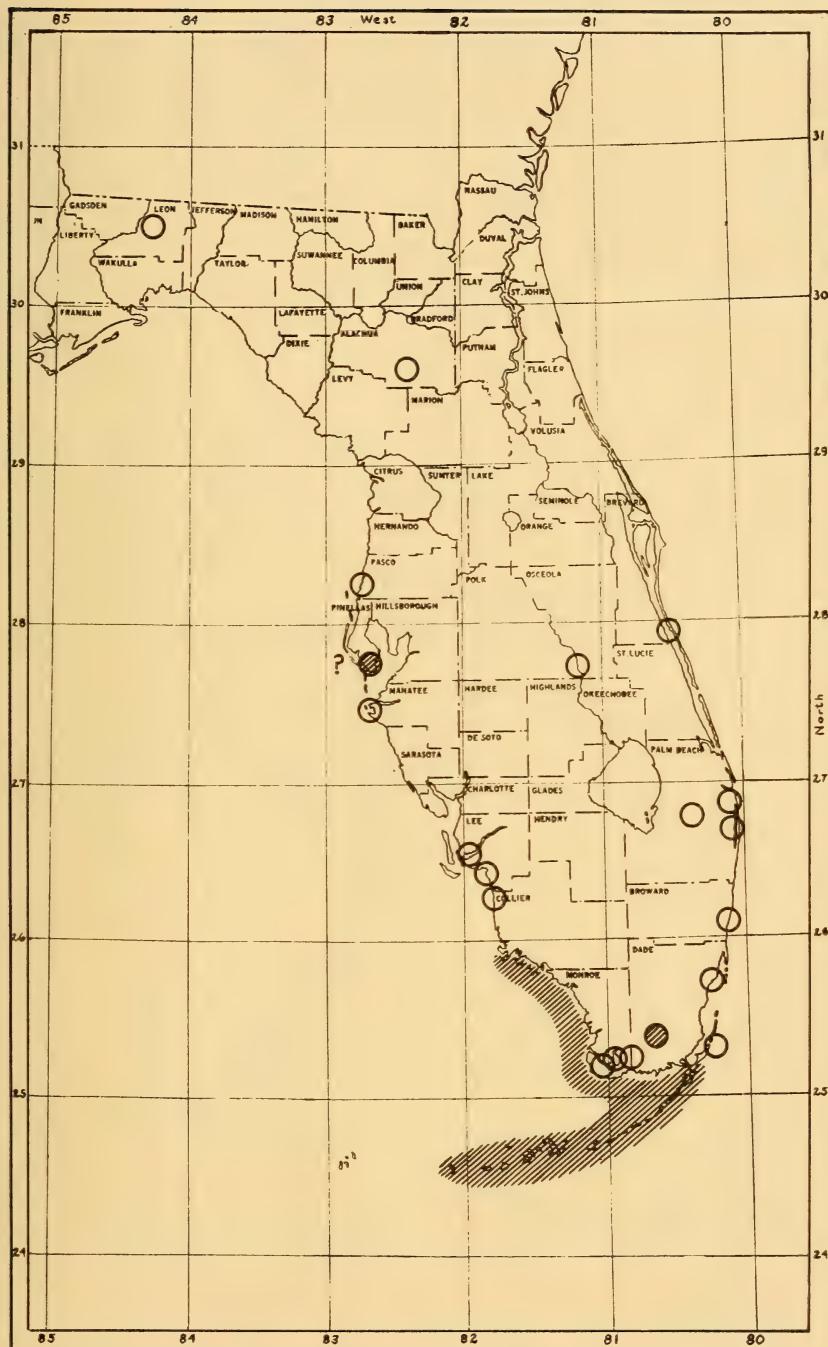
In no way is the difference between *Ardea occidentalis* and *Ardea herodias wardi* more marked than in their respective distributions. The latter breeds from the Florida Keys northward and westward to Beaufort County, South Carolina; Knox County, Indiana; Henry County, Iowa; and the eastern portions of Kansas, Oklahoma, and Texas (Cooke, 1913). The great white heron on the other hand has the most restricted distribution of any North American heron (consult Map I) and has not been known to venture farther north than Leon County, Florida.⁴ Audubon says, "It is truly surprising that a bird of so powerful a flight never visits Georgia or the Carolinas, nor goes to the Mainland." Its breeding range is confined to the keys of extreme southern Florida from Cape Romano south to Key West and east to Upper Matecumbe Key.⁵ Mr. Bent and Dr. Pearson, who have traveled

³ Mr. Bent's splendid Life Histories of North American Marsh Birds, 1926, did not appear until considerable time after the completion of the manuscript of this paper, but his summing up in that work of the case for the specific validity of the great white heron can add little to the force of his earlier remarks here quoted.

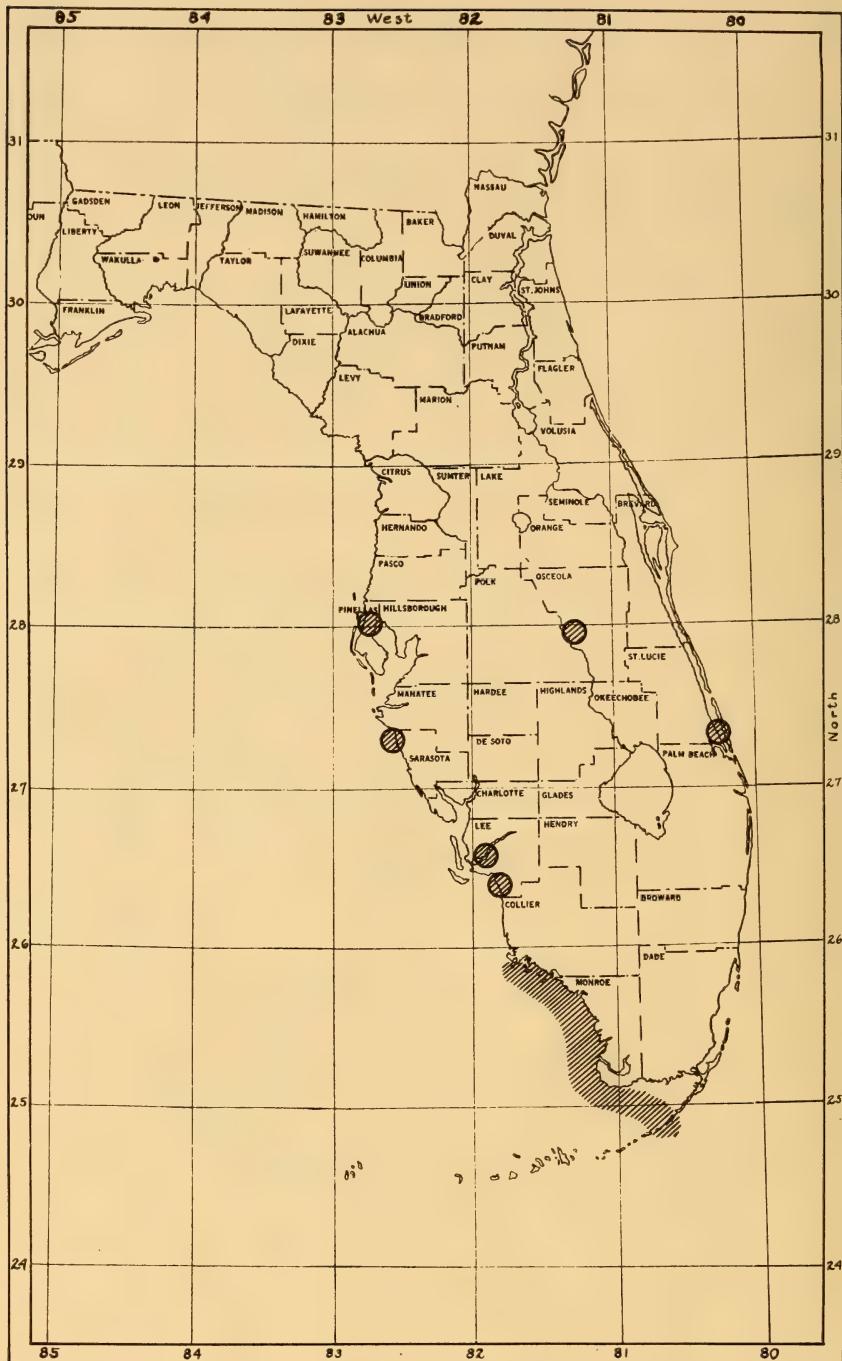
⁴ Brimley (1927) records the capture of a supposed great white heron near Durham, N. C., on July 8, 1926; but, while giving the record publicity, the Editor of The Auk casts some doubt upon it. My attempt to borrow the specimen for examination was not successful.

⁵ There are two published records of the breeding of the great white heron north of Cape Romano. The first appears in The Oölogist (1888, p. 150) under the title, "Notes from Alachua Co., Florida," and relates the taking of four sets of three eggs each near Archer. This, of course, is a plain case of mistaken identity. Although Chapman (1888) spent six months in the same county, with headquarters only 15 miles from Archer, and covered the same breeding season; and Baynard (1913), also with headquarters just 15 miles from Archer, recorded the breeding of 98 species of birds within a radius of about 20 miles; neither so much as mentions the great white heron. Nor did I, during a sojourn of five weeks in the vicinity of Micanopy, Gainesville, and Orange Lake, find any trace of it. However, the strongest argument against the acceptance of the Archer record is the text of the article itself.

The other record is by Pearson (1923), who writes that late in April, 1906, he found seven great white herons and four nests on Bird Key near St. Petersburg. This locality is so far beyond the normal breeding range of the species that I wrote to Dr. Pearson for confirmation of the record. Responding to my query he writes that while his 1906 identification was positive, on his visits to Bird Key in 1896, 1918, and on two or three other occasions, no great white herons were seen there. For this reason, and because of the great ease with which egrets are confused with the great white heron in the field, I believe that the record must be accepted subject to verification by specimens.

MAP I. FLORIDA RANGE OF *ARDEA OCCIDENTALIS*

Normal breeding range and records of isolated nestings are indicated by shading.
Records of occurrence north of breeding range are shown by plain circles.

MAP II. OCCURRENCE OF *ARDEA WÜRDEMANNII*

The shaded area indicates the region of usual occurrence — where the breeding range of *Ardea herodias wardi* overlaps that of *Ardea occidentalis* (cf. Map I). The shaded circles mark the capture of stragglers.

extensively in Florida, state that they have never seen the bird away from the coast. The only recorded exceptions to this rule are: A nesting reported by Howell (1921) at Royal Palm Hammock in the Everglades at the head of Taylor River, and just a few miles back from the coast; and the occurrence of stragglers at Ingraham, Gator, Bear, and West Lakes,⁶ Palm Beach Canal, Gainesville,⁷ Lake Jackson,⁸ and Cypress Lake, almost in the very center of the Peninsula. The last record would certainly be open to question had it not been published by such a well-known ornithologist as the late William Palmer (1901). The great white heron has been recorded on the Atlantic side of the Peninsula as far north as Micco, but there is no record of breeding on the East Coast above Upper Matecumbe Key.

A great white heron occurs in Cuba, the Isle of Pines, Jamaica, and Yucatan; but, as I am not prepared to discuss its relationships, I have confined my remarks to the Florida bird.

A glance at Map II will show that *würdemanni*, so far as known through the collection of specimens, is practically restricted to the breeding range of *occidentalis*, and has been most often taken where *occidentalis* is most abundant.⁹ All ten of the specimens of *würdemanni* at my disposal were taken within the circumscribed area of Florida Bay—the center of abundance of *occidentalis*. The Ward's heron, of course, breeds commonly throughout this entire region.

DISCUSSION

No author has given more attention to the Florida species of *Ardea* than Ridgway, as shown by his seven titles cited herein, yet even he has revised his conclusions more than once. His last expressed ideas are summed up in this quotation from the second edition of his Manual of North American Birds (1896):

“*A. wuerdenni* is probably merely an intermediate plumage

⁶ All four of these lakes lie in the Cape Sable coastal swamp. Gator Lake is farthest inland—almost two and a half miles from Florida Bay—but is strongly impregnated with salt; the other three have direct connection with sea water.

⁷ This unpublished record is courteously tendered me by Mr. Oather C. Van Hyning, who saw the bird at close range in Bivan's Arm, about two and a half miles south of Gainesville, on May 9, 1926.

⁸ An adult female great white heron was collected on Lake Jackson, Leon County, October 4, 1925, by Mr. Herbert L. Stoddard, who has graciously placed the record at my disposal.

⁹ Mr. Ridgway's *sight* record (1878, p. 235) of *würdemanni* near Mount Carmel, Illinois, is unique, and need not be considered.

connecting *A. occidentalis* with *A. wardi*, the three forms doubtless merely color-phases of one species, for which *A. occidentalis* is the older name."

This statement stood without definite question until Oberholser (1912) published the opinion that *würdemanni* is a hybrid between the specifically distinct forms *Ardea occidentalis* and *Ardea herodias wardi*. This in turn was put on the defensive by Bangs (1915), who formally proposed that *Ardea herodias wardi* Ridgway and *Ardea würdemanni* Baird be considered synonyms of a new combination, *Ardea herodias occidentalis* Audubon. Unfortunately, Mr. Bangs produced no supporting evidence other than analogies, and these substantially the same that were presented by Mr. Ridgway thirty-seven years before.

The herons cited by these authors as examples of dichromatism analogous to the case of the great white heron are: *Demigretta sacra* (Gmelin), the reef heron; *Florida cœrulea* (Linnæus), the little blue heron; and *Dichromonassa rufescens* (Gmelin), the reddish egret.

Because of inadequate material, I am unable to discuss the first; but to my mind the white dress of *Florida cœrulea* presents no parallel whatever with the plumage of the great white heron. Although the little blue heron may sometimes breed while still clothed in white (rather an unusual occurrence, I believe), that fact *per se* is no indication of maturity, for other birds, the redstart and the orchard oriole, for instance, are known to breed in immature livery. The nestlings of the little blue heron are invariably white, while Mr. Ridgway himself states that he has "never seen a specimen in the blue plumage which was not unmistakably an adult!" Moreover, some specimens show plainly the moult from white to blue plumage; and but rarely does any white bird possess the plumes of the adult. Withal, it would seem that the white plumage of *Florida cœrulea* is primarily an indication of youth even though it may be sometimes retained in age. Such is not the case with *Ardea occidentalis*, which is hatched a creamy white and remains immaculate throughout life.

Although some individuals of the reddish egret are said to show an intermediate stage of plumage, it seems to be the rule that they are either pure white ("pealei") or of the rufescent type. Ap-

parently there are no specimens homologous to *Ardea würdemannii*. Here again the parallel with "*Ardea herodias occidentalis*" breaks down; for this form, as conceived by its proponents, exhibits three phases, corresponding to *occidentalis*, *wardi*, and *würdemannii* of authors, whereas in the reddish egret there are only two. Moreover, the plumes of white reddish egrets that I have examined show the same superb development as in the rufescent birds, but I have yet to see a great white heron wearing the well-developed plumes of the Ward's heron.

Were *wardi* and *occidentalis* color-phases of a single dichromatic species one would expect, reasoning from the cases of the little blue heron and the reddish egret,¹⁰ most of the blue individuals to run true to the dark or normal phase (*wardi*), and the variations, such as washing or spotting, to occur in the white phase (*occidentalis*). The reverse is actually the case, for on the Florida Keys the great white herons are wholly white (with rare exceptions), whereas I have seen no big blue herons from this region that could be considered pure *wardi*. In other words, the big herons are either white or paled blue—rarely pure blue (i. e., *wardi*), and never bluish-white or white mottled with blue.

Messrs. Ridgway and Bangs in searching for analogies have touched upon erythrism and melanism; but it appears to me that these phenomena are not comparable with white and blue dichromatism, for the reason that they are not manifested in the same way, and therefore I would not bring into the discussion the screech owl and Cory's least bittern. For the same reason, but more especially because the true status of the forms is still in doubt, I refrain from discussing *Butorides brunnescens* (Lembeye) and *Certhneis sparverioides* (Vigors).

On the general subject of erythrism and melanism, however, it may be observed that such phenomena result usually from a simple increase in pigments already present and not from a change in the kind of pigment (the screech owl, of course, is a notable exception). Erythrism seldom completely obscures the pattern of the subject, and this is often true of melanism also; and the variation in intensity of red or black is almost infinite in any given

¹⁰ All white *Florida carnea* have bluish tips to the primaries, and usually a wash of blue on other parts of the body as well; and intermediate reddish egrets seem to be more often white birds with some blue in the plumage than bluish birds with white.

erythrismal or melanotic species. On the other hand, the inheritance of white in the mixed offspring of *wardi* and *occidentalis* is manifested either by a complete blotting out of all color and pattern or by only a slight paling of an otherwise apparently normal blue individual. The gap between the white and the blue birds is enormous. Thus there are no degrees of white as there are of red in the screech owl or of the black in the fox squirrel.

Let us turn now from the discussion of analogies and consider a concrete difference between *Ardea herodias wardi* and *Ardea occidentalis*, namely, the form and length of the occipital plumes. These plumes average 80.5 mm. longer in *wardi* than in *occidentalis*; in the former they are always long-ligulate, while in *occidentalis* they are acuminate-lanceolate. As has been shown, these differences are constant through a series of 24 specimens of each species.

Now, some have held that a white feather (of an albinotic bird) is weaker than a colored feather, and that, therefore, the plumes of the white birds of a dichromatic species would tend to be reduced or even to drop out; but this is refuted by the plumes of the white reddish egret, which are as fully developed and vigorous as those of the bird of normal plumage. By the same token an albinotic bird would be a weakened individual and less fit than its normal associates, and this is actually claimed by such to be true. At any rate, many albinos appear in normally black species, such as crows and blackbirds, yet there is no white phase among them. Were the great white heron an albinotic phase of the Ward's heron,¹¹ it would be difficult to explain its hardiness and ferocity, or its abundance. Rather, one would expect it to die out instead of establishing a regular phase within the species. Therefore, I cannot believe that there is any question of albinism, in the genetic sense, involved in the case.

It may be that a factor for short occipital plumes is linked with the factor for whiteness, but the determination of that point would not help in the solution of the problem of dichromatism. Unfortunately, either factor would behave in essentially the same manner in the crossing of a white and a blue bird whether they

¹¹ It is certainly not a true albino, for it has the same bright yellow eyes common to the species of *Ardea*, *Florida*, and other heron genera, and its legs are blackish.

represented different species or merely dichromatic forms of the same species. Therefore, the finding of a white nestling and a blue nestling in the same nest indicates little more than that at some past time there has been a fruitful mating between a white and a blue heron.

Theoretically, provided white or blue were fully dominant, the F_1 cross would be outwardly pure white or pure blue, and the F_2 birds would be some blue and some white, according to Mendel's law of segregation. Practically, however, there are no pure hybrid strains that we can recognize; the mixed birds have crossed back with *wardi* and with *occidentalis*, and have bred with each other, and have been doing this so long that there is no knowing what the inheritance of a given individual may be. As we have seen, there are no true intermediates between the blues and the whites, and apparently there are but a few *pure blues* (*wardi*) within the breeding range of the whites.

The preponderance of seemingly pure *occidentalis*; the fact that those birds in which mixed blood is recognizable (i. e., *würdemannii*)—mixed blood is never recognizable in the immaculate white birds) are always distinctly blue, but modified in the direction of *occidentalis*; and the fact that even the eggs of *würdemannii* suggest this same modification towards *occidentalis*, led me to believe that *occidentalis* is actually prepotent in the cross with *wardi*. But this belief is not supported by Dr. Sumner, and I defer without question to his knowledge and experience in the field of practical genetics. After critically reading my entire manuscript, he concedes the probability of the specific distinctness of the blue and the white herons, but finds the meager genetic evidence somewhat conflicting and altogether inadequate for proving the case either pro or con.

Much light might be thrown on the problem by cross-breeding great white herons and Ward's herons under strict control—an undertaking, however, that would be extremely difficult if not impossible. But if such experimental work could be carried out by a trained geneticist, it would be highly desirable, for, even if it did not produce facts new to the geneticist, it could not fail to lighten the burden of the vexed systematist. Notwithstanding the fact that workers in these two fields of science often hold quite divergent

views regarding the proper definition of a species, I believe that we must turn more and more to genetics in order to understand the full significance of the phenomena we would systematize in our studies of relationships and geographical distribution.

Little need be repeated here regarding the different behavior of the great white heron and the Ward's heron, though one or two points should be touched on a bit further. It has been noted that observers are in general agreement on the greater wariness of *occidentalis*. Some may be inclined to account for this on the assumption that the white birds realize their greater conspicuousness; but it is doubtful whether there is actually much difference in visibility between the two birds, living as they do absolutely exposed on the mud banks. Moreover, Scott's account (1889) indicates that *würdemanni* partakes of this shyness of *occidentalis*, and as *würdemanni* is very little lighter in the field than *wardi* it is not reasonable to try to apply here also the theory of realization of greater conspicuousness. Furthermore, I have observed no difference in wariness between the white and the blue individuals of *Florida cærulea*.

It may be asked how great white herons and Ward's herons could ever have come to mate if the great white heron is so fierce and so intolerant of its congener.¹² But may not propinquity and the procreative urge bring about as strange alliances among birds as among humans? Once the mating were accomplished, the resulting hybrids would be more acceptable to either species than the species to one another, and thus would be started the chain of inter-breeding that has led to the chaotic condition to be found on the Florida Keys today.

Lastly, I would emphasize again the fact that the great white heron keeps almost strictly to salt water, where it forages upon the vast expanses of mud exposed at low tide, while the Ward's heron ranges all over the Peninsula. The maritime habitat of the great white heron may be determined by its food habits, or by its extreme wariness which leads it to haunt only places where its view is unobstructed for long distances—a condition not fulfilled by inland creek and river banks. Be that as it may, I can find no cause that would restrict the white phase of a dichromatic species

¹² I am impelled to remark that I have not observed this intolerance.

almost absolutely to salt water while the blue phase of the same species ranges at will over both maritime and continental habitats.

SUMMARY AND CONCLUSIONS

In summary it may be stated that:

- (1) In *Ardea occidentalis* the occipital plumes are either greatly reduced, in comparison with similar plumes of *Ardea herodias wardi*, or are absent altogether. When present they are of a different form from those of *wardi*.
- (2) The scapular and jugular plumes of *occidentalis* show less development than similar structures of *wardi*.
- (3) A small series of measurements indicates that there is a small but absolute difference between *occidentalis* and *wardi* in relative and proportionate size of bill.
- (4) All adult big blue herons from Florida Bay exhibit a paling of colors or shortening of plumes, or both, whereas such modifications are not found in specimens from localities beyond the range of *occidentalis*.
- (5) All great white herons (with rare exceptions) are immaculate.
- (6) Great blue herons (more properly, *würdemanni*) eggs from the Florida Keys exhibit the same form as eggs of *occidentalis*; those taken at Bassenger are more pointed. (This difference might not hold in a larger series.)
- (7) *Ardea occidentalis* is reputed to be the shyest of all the American herons—much shyer than *wardi*.
- (8) *Ardea occidentalis* is said to be much fiercer and more pugnacious than *wardi*; captive great white herons are said to kill captive Ward's herons, whereas they exhibit no animosity towards their own kind.
- (9) *Ardea occidentalis* is considered diurnal in its feeding habits, while *wardi* feeds both by day and by night. (But Mr. Bent has aptly asked, "Who could ever get near enough to a Great White Heron to see it feeding at night? Perhaps it does. Who knows?")
- (10) *Ardea occidentalis* is strictly maritime and confined to southern Florida. Stragglers from the seacoast are rare, and

there is only one record of breeding on the mainland. *Ardea herodias wardi*, on the other hand, breeds all over the State, completely overlapping the range of *occidentalis*, and is in no wise restricted to salt water either in its feeding or breeding habits.

(11) All ten specimens of *Ardea würdemannii* at my disposal were taken within the circumscribed area of Florida Bay—the center of abundance of *occidentalis*.

Reasoning from the facts herein presented I conclude:

(1) That *Ardea occidentalis* Audubon is a distinct species, immaculately white, and without a colored phase; (2) that *Ardea herodias wardi* Ridgway possesses no white phase; and (3) that *Ardea würdemannii* Baird is simply a hybrid resulting from the crossing of these two species in the restricted area where their breeding ranges overlap. Such interbreeding has been going on for a long period of time; and, as a consequence, it seems doubtful whether any big blue herons of pure blood are now to be found in Florida Bay—unless they be migrants or stragglers from other places. What effect the indefinite continuance of this process may produce on the species involved, only time can tell; but it is evident that, now at least, white, which in closely related dichromatic species is without taxonomic importance, in this case becomes a character of specific value.

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HOLT—STATUS OF ARDEA OCCIDENTALIS

35

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